CLIMATE CHANGE AND ITS IMPLICATIONS FOR THE TERRESTRIAL VERTEBRATE FAUNA

by PHILIP STOTT

Summary

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A limited number of studies of the biology of a variety of species of terrestrial vertebrates is used to speculate about their responses to climate change as predicted by global circulation models. Dramatic changes in the distribution and abundance of animals in Australia that has already occurred consequent to European settlement is noted Speculation about the impact of climate change on the relative abundance of mammals and reptiles, range changes of kangaroos, rabbits in arid areas, food security of the Spinifex Hopping Mouse, competition between two species of skinks, and disease transmission is included. Nest-site selection by tortoises and social structure of foxes are given as two examples where behavioural plasticity demonstrates some capacity to cope *in situ* with the effects of climate change, but the ability of most terrestrial vertebrates to track rapid climate change across different substrates is questioned. Reservations are expressed about the knowledge base upon which the speculations are based. For very few species is a suite of studies available to compare detailed data on distribution and abundance with climate over a wide geographical range, backed up with biological information sufficient to explain the mechanisms by which the species interact with their environments.

KEY WORDS: Climate change, mammals, reptiles, Testudines, abundance, distribution, rainfall, drought, disease, *Macropus giganteus*, *Macropus fuliginosus*, *Oryctolagus cuniculus*.

Introduction

Some 6000 years ago, within the span of 100 years, the vegetation at Cold Water Cave, Iowa, changed from forest to prairie (Dorale *et al.* 1992). The changes were associated with a temperature rise of c. 3°C, and with such a complete change in vegetation structure must have come a profound change in the vertebrate fauna of the locality. It may be, during the next century, that similar dramatic changes in biota will result from an anthropogenically-enhanced "greenhouse" effect. The terrestrial vertebrate fauna of Australia has already undergone profound changes as a consequence of European settlement (Recher & Lim 1990); climate change would compound the impacts of introduced competitors and predators, destruction and fragmentation of habitat, altered fire regimes, hunting, and diseases.

Realistic predictions about the impact of climate change on the distribution and abundance of terrestrial vertebrate species require a foundation of information from several sources. Essential are detailed forecasts from climatologists; predictions about changes in the distribution, composition, and productivity of plant communities and other elements of food webs; and detailed information about the present distribution, abundance, physiology, and ecology of vertebrates. The temporal scale of possible changes should also be considered.

The sentiments expressed in this paper are complementary to those expressed in essays by Arnold (1988), Busby (1988), Graetz (1988), Main (1988), and Possingham (1993). The paper augments previous contributions by exploring some examples of the mechanisms by which climate change might affect vertebrates. It is a speculative paper; the scenarios are presented with the intent of illustrating the level of complexity, rather than making confident predictions about the outcome. The predictions are weakened because a single study of a local population over a short period of time is not necessarily representative of the biology of a species during all seasons and over the whole of its range (see Kemper *et al.* 1987), and the range and habitat of a species as observed to date do not necessarily represent accurately the realised environmental niche of the species, nor this in turn its fundamental niche (Possingham 1993). In addition, the predictions of global climate models are not considered to be reliable at the regional level (Gordon *et al.* 1992). As the number of logical steps increases, so the errors are summed.

The paper reviews those climatic predictions of particular importance to animals, uses some examples to explore the mechanisms by which climate change might affect terrestrial vertebrates, then examines the capacity of animals to cope with the predicted changes.

Predicted climate changes

Evidence from climate models indicates that emissions of "greenhouse" gases into the atmosphere

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will cause global warming of 0.3 (range 0.2-0.5) °C per decade, and associated changes in patterns of precipitation (Houghton et al. 1992). Whilst the general predictions of the models are broadly accepted, the issue is complicated by the lack of clear observational evidence of changes attributable with certainty to an enhanced "greenhouse" effect. On examining records of meteorological observations, Nicholls & Lavery (1992) were not able to identify any clear trends in rainfall at reliable meteorological stations in South Australia up until 1988. Although Burrows & Staples (1991) note a warming trend in South Australia since 1950, they cautioned that the trend was "close to the bounds of past experience". Models are not consistent in their predictions of seasonal changes in temperature patterns for South Australia (see Boer et al. 1992; Gates et al. 1992); at the present state of refinement of the general circulation models such uncertainties in timing, magnitude, and regional patterns are well recognised (Houghton et al. 1992).

Rainfall has a major influence on food supply for vertebrate species, particularly in arid areas. Haarsma et al. (1993) predict a global increase in tropical disturbances. At present, some of these disturbances extend into northern South Australia as tropical-extratropical cloudbands (TECBs), and as a result heavy rain falls on an average of nine days per year (Kuhnel 1990). However, the distribution and extent of the rainfall is erratic. Gordon et al. (1992) cautiously report the results of simulations which indicate changes in daily rainfall intensity across Australia, particularly in summer, in the form of increases in the frequency of heavy (12.8-25.6mm, c. 31%; >25.6 mm, c. 95%) rainfall days, an c. 15% decrease in the frequency of light (<6.4 mm) rainfall days, and a decrease in the number of rain days. Whetton et al. (in press) review the predictions of five global circulation models: four predict increasing summer rainfall over the whole of South Australia (all five predict increasing summer rainfall over much of the far north), and four predict a decrease in winter rainfall over most of South Australia.

A weakness of the models is that they do not take into account all major known influences on climate. The El Niño Southern Oscillation (ENSO) phenomenon is not coupled with the major global circulation models (including the CSIRO9 model) despite its influence on variability of rainfall in Australia (Whetton et al. in press). ENSO is of particular importance to the recruitment of many arid zone species (Austin & Williams 1988; Graetz et al. 1988). The influence of ENSO needs to be considered in addition to changes predicted to accompany the enhanced greenhouse effect (Walker et al. 1989). The issue is further complicated because ENSO itself may be affected. If increased CO₂ works to equalise temperatures in the waters of the eastern and western Pacific Ocean, ENSO would be weakened (Rind 1991), thus tending to reduce climatic variability in eastern Australia and countering to some extent the predictions outlined above.

Direct effects

Direct effects of climate on vertebrates should be more readily elucidated than would be the case with indirect effects. Two examples are presented of direct effects of climate on reptiles. The first is the process of temperature-dependent sex determination, and the second is the influence of temperature on the distribution of testudines (turtles and tortoises). Both examples demonstrate that the knowledge base is inadequate even in this more straightforward category.

Temperature-dependent sex determination

Temperature-dependent sex determination (TDSD) has been demonstrated in many species of testudines (e.g. Mrosovsky et al. 1984), crocodilians (e.g. Webb et al. 1983), an agamid (Charnier 1966 vide Bull 1980), and a gekkonid (Wagner 1980). Slight (<2°C) departures from pivotal incubation temperatures may result in entirely male or entirely female sexual phenotypes, even in some of the species which have heteromorphic sex chromosomes (Servan et al. 1989). Some species have two thresholds, with males resulting from intermediate and females from extreme incubation temperatures (Yntema 1976; Webb & Smith 1984). TDSD has been demonstrated to occur in an Australian crocodilian (Webb et al. 1983), an Australian freshwater/estuarine testudine (Webb et al. 1986), and Australian marine testudines (Limpus et al. 1985). In contrast, it does not occur in several Australian freshwater testudines, including species found in South Australia (Georges 1988; Thompson 1988a). Preliminary studies suggest that TDSD occurs in at least four Australian agamids (G. Johnston pers. comm.).

The influence of environmental temperature on sex ratios is a mechanism by which climate change can directly affect the distribution of reptiles. Species with TDSD would be more susceptible to rapid climate change than species without TDSD. Webb & Smith (1984) noted variation in sex ratios of Crocodylus johnstoni hatchlings in the field, and speculated that it was due to the interaction between TDSD and geographic differences in mean air temperatures. In a warmer climate, the effect might be to skew the sex ratio completely, blocking reproduction, and thus leading to the local extinction of the species. Such a scenario has been advanced by Pieau (1982) as a possible reason for the extinction of many Mesozoic reptiles.

Distribution of testudines

Testudines, which require external sources of heat for metabolic activity, are limited in latitudinal distribution by temperature. However, mean annual temperature is far too crude a measure to predict limits to distribution. Length of the growing season has been generally accepted as a limiting factor, since at the latitudinal limits of distribution adults may not have enough time to accumulate sufficient energy reserves to survive the winter (MacCulloch & Secoy 1983). Alternatively, distribution may be limited by the ability of hatchlings to survive overwintering in the nest (Breitenbach *et al.* 1984; Congdon *et al.* 1987). Obbard & Brooks (1987) suggest that a critical factor is temperature during the maturation of ova, which requires the accumulation of heat units over spring sufficient for successful reproduction. I suggest another possibility; that distribution is limited by the probability of ambient temperatures being sufficiently high during the nesting season to permit the energy expenditure necessary in digging the nest chamber, an activity recognised as being energetically demanding (Congdon & Gatten 1989).

To predict the effect that climate change would have on a species requires detailed knowledge both of the nature of the change in climate and of the mechanisms by which climate change would affect a species. In testudines, we need to know which of the above hypotheses is acceptable before we know whether to examine number of days between threshold temperatures, nadir winter temperatures, number of spring days above a temperature threshold, or the probability of occurrence in spring of spot temperatures above a threshold.

Indirect effects

Effects mediated by other factors are inherently more complex than direct effects. Attempts at predicting changes in animal distributions based on detailed analyses of complex mechanisms which include consideration of matters such as physiology, population dynamics, interspecific interactions, behavioural changes, and microhabitat conditions are fraught with potential for error. An alternative is to identify a smaller suite of influences which drive the system and determine the end result. Nix (1982) saw climate as the major determinant of the distribution of terrestrial organisms, and several authors have used various climatic indices to explain the diversity and abundance of particular Australian biota. Of particular value are those rare studies which compare detailed data on distribution and abundance with climate over a wide geographical range. Both mechanistic and deterministic explorations follow.

Relative abundance of mammals and reptiles

Arid Australia already has a more diverse and abundant reptile fauna than arid areas in North America and Africa (Pianka 1985). In part, the diversity and abundance of the reptiles is attributed to the high variability of rainfall which is a feature of the Australian inland (Morton & James 1988). Proposed changes in climate might therefore be expected to lead to an increase in the diversity and abundance of reptiles relative to mammals.

Not all mammals would necessarily be adversely affected. For the large arid areas of Australia, net annual productivity and hence the carrying capacity expressed as total biomass of vertebrates is related to annual rainfall (Burbidge & McKenzie 1989). However, the species composition of the total biomass is largely determined by the predictability and distribution of the rainfall, rather than its amount. Patchy rainfall favours birds, bats, and mobile large mammals such as kangaroos (Burbidge & McKenzie 1989) which are physically capable of moving long distances to environments made favourable by recent heavy rains. Irregular rainfall favours reptiles, which have very low field metabolic rates relative to mammals (Nagy 1987) and can survive for long periods without food (Morton & James 1988). A change in rainfall patterns to fewer days with rain, a lower probability of light rainfall, and an increase in the frequency of heavy rainfall would not have a great impact on mobile animals, but would favour reptiles over small mammals. Small mammalian cellulose-dependent herbivores would be particularly disadvantaged; they are vulnerable because their energy intake is limited by their gut size. This represents a similar proportion of the size of the individual as in larger animals, but the energy expenditure for maintainance of body temperature must be relatively higher than for larger mammals which have a lower surface area to body mass ratio (Morton 1990). They are also limited by their restricted mobility in their ability to exploit a patchy environment; and they are most vulnerable to competition from rabbits (Burbidge & McKenzie 1989; Morton 1990).

It could be argued that the balance between the diversity of reptilian and mammalian species as at the time of European settlement was determined in some prior, more severe period of aridity (such periods are known from prehistoric times- see Singh 1981), and therefore the balance would not be affected by a further increase in temperature and in the variability of rainfall. Further, any mammals which might have been affected are already extinct as a consequence of European settlement. The counter argument is that effective aridity in the future may be more extreme than in recent evolutionary time. Climatic aridity (wherein increased evaporation is in excess of increased rainfall) may be compounded by "emulated aridity" because of the

consequences of the removal of primary productivity from the arid system in the form of livestock and livestock products (Burbidge & McKenzie 1989), and the sequestration within the arid system of primary productivity and nutrients in the tissues of livestock and rabbits. Thus the resources available to native vertebrates would be significantly diminished, particularly during the resource "bottlenecks" of droughts, and in drought refuges (see Morton 1990).

Range changes of kangaroos

The responses of kangaroos can perhaps be predicted with a little more confidence than those of other vertebrates. Many studies of kangaroos have been undertaken, including thorough studies of their distributions (Fig. 1a) as part of the basis for managing populations which are commercially harvested.

Caughley *et al.* (1987) have demonstrated that the distribution of three species of kangaroos is, in the major part, determined by climate. Whilst the distributions are directly determined by land use and the availability of food, water, and shelter, these attributes are in turn greatly influenced by climate. The distributions of the two grey kangaroos, the Eastern Grey Kangaroo (*Macropus giganteus*) and the Western Grey Kangaroo (*M. fuliginosus*), are closely associated with the seasonality of rainfall; they overlap in areas of uniform seasonality of rainfall, but *M. giganteus* occurs in areas where summer rainfall predominates, and *M. fuliginosus* occurs in areas where winter rainfall predominates. The Eastern Grey tolerates higher seasonal temperatures than the Western Grey provided

that there is summer rainfall. Both require a heterogenous habitat with shelter being an important component (see Hill 1981, Cairns *et al.* 1991). The distributional data have been used by Walker (1990) to develop an integrated modelling and mapping system which could be used to predict and map changes in distribution consequent to climatic change. Caughley *et al.* (1987) suggest that climate change in the past has influenced the distribution of macropods: it is therefore reasonable to use their conclusions to predict the distributional responses of these three species to future climate change.

If, as predicted (above), the winter rainfall zone contracts to the south and temperatures rise, the distribution of the Western Grey Kangaroo would also contract to the south (Fig. 1b). Perhaps more remarkable might be changes to the distribution of the Eastern Grey Kangaroo. At present the species occupies two small and widely separated areas in South Australia, but these are minor projections into this State of a distribution whose western boundary runs along or just to the east of the State's eastern borders (Caughley *et al.* 1984). *M. giganteus* could extend a considerable distance to the west of its present distribution, and hence across the north of South Australia to occupy suitable habitats in the northern part of the present range of *M. fuliginosus*, if certain conditions are met. They are that summer rain becomes more common in northern South Australia, that reliable water is provided by increased frequency of heavy rainfall and/or livestock water supplies, and that habitat heterogeneity persists in the face of climate change.
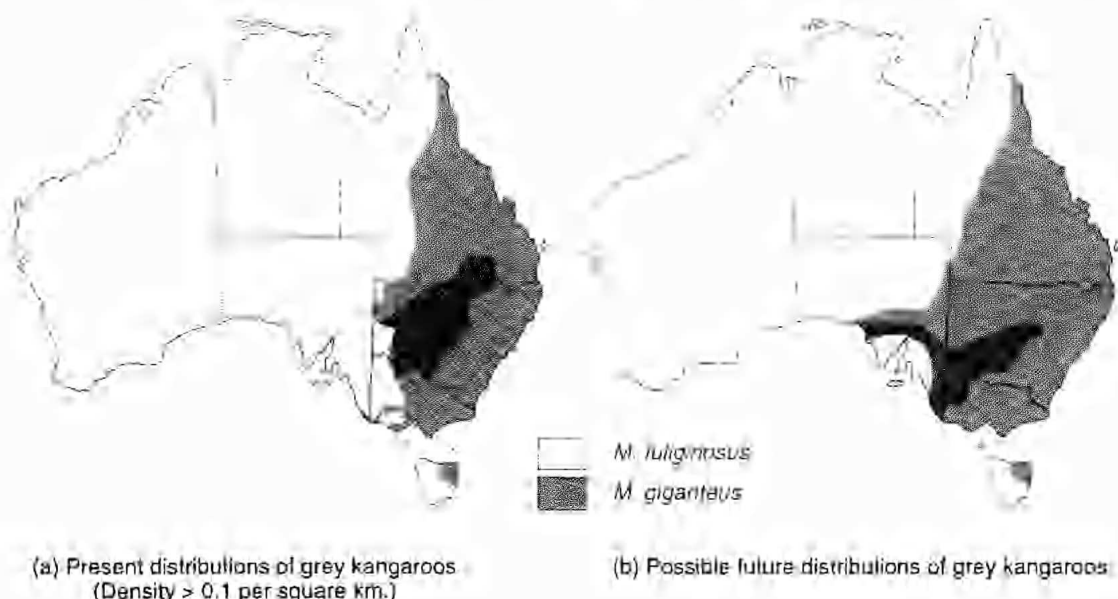

M. fuliginosus
M giganteus

(a) Present distributions of grey kangaroos
    (Density > 0.1 per square km.)

(b) Possible future distributions of grey kangaroos

Fig. 1. (a) Present distributions of grey kangaroos. (b) Possible future distributions of grey kanagaroos. Adapted from Cairns *et al.* (1991), Caughley & Grigg (1981), Caughley *et al.* (1983), Caughley *et al.* (1984), Short *et al.* (1983).

Survival of rabbits in arid areas

In arid Australia, the European Rabbit *Oryctolagus cuniculus* is decreasing the probability of survival of small perennial plants during droughts, and having a profound effect on the recruitment of some species, sufficient in time to eliminate them from the landscape (Lange & Graham 1983; Cooke 1987). The response of the rabbit to climate change is therefore of particular importance.

Historical records show that rabbits in arid areas have been severely reduced in numbers during past droughts (Griffin & Friedel 1985), and may, under drought conditions, become extinct over large areas (Myers & Parker 1975). Recruitment is most unlikely under drought conditions (King *et al.* 1983), and prolonged droughts such as the 1958-64 and 1925-38 droughts at Alice Springs (Griffin & Friedel 1985) test the longevity of the species (see e.g. Dunsmore 1974). Even so, a few rabbits survive in refuges. The quality of the refuges is determined by their ability to harvest and store water and nutrients flowing from larger areas of the landscape (Morton 1990) such that run-on from light rainfall is sufficient to stimulate some plant growth during the drought period (Ludwig 1987). At Witchitie, South Australia, Cooke (1982) noted that a sharp fall of little more than 5mm of rain might be sufficient to yield run-off which, if concentrated along drainage lines, would ensure that succulent food in the form of chenopod shrubs would be available to rabbits living in warrens along those drainage lines. Once heavy rain falls (> 20 mm near Carnarvon, Western Australia; King *et al.* 1983), rabbits begin to breed, and can expand from the refuges to recolonise the bulk of the landscape.

Heavy rainfalls are rare in the Australian arid zone; whole years may pass without a rainfall event $\geq$ 12.5 mm (Stafford Smith & Morton 1990). Light falls are more common, but it has been predicted (see above) that the heavy falls would become more common, and light falls somewhat less common. Hence, droughts are likely to be shorter in duration, but the refuges which sustain the residual rabbit population during droughts would be a little less reliable. With a coincident rise in temperature exacerbating the severe physiological stress experienced by rabbits under present summer conditions (Hayward 1961), local extinction becomes more likely during droughts, but, with decreased return times for heavy rain, plagues might be expected more frequently in those areas where rabbits survive.

Vegetation changes consequent to the increased variability of precipitation might not favour rabbits. Rabbits are found in chenopod shrublands, but the majority of the feed is provided by the short grasses and forbs between the shrubs; the chenopods are eaten only during droughts (Hall *et al.* 1964; Griffin & Friedel 1985). Under conditions of increased climatic variability, perennial plants would be favoured over ephemeral plants (Stafford Smith & Morton 1990), so rabbit populations could be expected to become less dense unless palatable perennial grasses such as *Themeda* sp. replaced annual grasses and forbs. Further exploration of this scenario would need to take account of a potential southern extension of the dominance of C_4 over C_3 grasses (Henderson *et al.* in press), the relative importance of C_3 and C_4 grasses to rabbits, and the implications for rabbits of a change in the seasonal distribution of rain towards summer rainfall in arid areas of South Australia.

Food security for Spinifex Hopping Mouse

Notomys alexis, the Spinifex Hopping Mouse, is widely distributed through sandy areas of northern South Australia, mainly in association with spinifex grasses (Watts & Aslin 1981). A major component of its diet is seed (Finlayson 1940), and from the carbohydrate in seed it is able to derive sufficient metabolic water to survive indefinitely; one female is known to have reared a single young without supplementary water (Baverstock & Watts 1975). Hence the regularity of seed production would influence survivability of *N. alexis* in northern areas of the State. Seed production may be influenced by soil moisture, temperature, and CO_2 levels, and two mechanisms by which *N. alexis* might be advantaged are explored.

Soil moisture is one of the most important climatically determined variables for grasslands (Pittock 1993) and hence for species such as *N. alexis* which depend in large measure on grasses (MacMillan & Lee 1969). Walker *et al.* (1989) anticipate that mean soil moisture is likely to diminish in northern South Australia, although at present the reliability of predictions is questioned (Vinnikov 1991; Pittock 1993). More important for seed production are episodes of higher soil moisture following heavier rainfalls, which are predicted (above) to become more frequent. Thus pulses of seed supply may become more frequent, and support denser populations of *N. alexis*.

The rate of growth and the speed at which seed development occurs following rains may be accelerated. Imai *et al.* (1985) observed increased seed yield per plant for rice grown under enhanced greenhouse conditions. Gifford (1979, 1988) predicted that wheat yields in areas with more strongly seasonal rainfall would increase as a result of the enhanced "greenhouse" effect, and that some grain growth would become possible under conditions of aridity which currently preclude any yield. The factor influencing yield was stimulation to plant growth by both increased CO_2 and warmer temperatures, which would result in a shorter growing season such that the grain was more likely to be filling under a favourable soil moisture regime. Enhanced efficiency of water use would also occur due to partial stomatal closure (Chaves & Pereira

1992). Thus droughts as perceived by *N. alexis* may be ameliorated by the supply of some seed when none would be otherwise be available.

Australian arid-zone soils are generally infertile (Morton 1990), and nutrient limitation may counter growth-stimulating mechanisms. Although seed production may be limited by the availability of phosphorus, nitrogen is less likely to be limiting for C_1 plants, but a likely corollary is that the protein content of their seeds would be lower [see Conroy 1992]. *N. alexis* would not be disadvantaged, as it is more likely to survive drought on low protein diets which obviate the need to expend water to dispose of waste nitrogen (MacMillan & Lee 1969).

Competition between Ctenotus *species*

Many of the 70 species in the scincid genus *Ctenotus* are associated with spinifex (Cogger 1992), and it is not unusual for several species to be syntopic, suggesting fine niche separation between them. If climate influences the niche separation, climate change may affect the balance between the species.

Ctenotus helenae and *C. pantherinus* are two species occurring sympatrically in the far north-east of South Australia; Pianka (1969) noted that they shared similar niches, and suggested that *C. pantherinus* would be excluded by *C. helenae* but for its reproductive capacity. James (1991a) found a high degree of dietary overlap between the two species, and noted that dietary overlap in *Ctenotus* was highest during the driest period of his study. There is evidence to suggest that the separation between these two species is based on their thermal responses; Pianka (1986) found *C. pantherinus* to have a lower mean body temperature than *C. helenae*, and James (1991b) speculated that *C. pantherinus* (and *C. brooksi*) can be active at winter temperatures which preclude activity by *C. helenae* (and other *Ctenotus* species). This permits *C. pantherinus* and *C. brooksi* to begin reproduction earlier than the other species. If activity at different temperatures is critical either for maintaining stable niche separation or for sustaining a mechanism of oscillating disequilibrium between the species, an increase in temperature during winter may result in competitive exclusion of *C. pantherinus* by *C. helenae* in those areas where they are sympatric.

Epidemiology

In stable ecosystems, there is generally a significant level of accommodation between host populations and disease-causing agents, particularly if they have co-evolved. However, transmission of infectious disease is a dynamic process, and in many cases is dependent on the capacity of the infectious agent to survive outside of the host. Helminth parasites often have obligatory larval stages which may survive for long periods on the ground, and thus be susceptible to climatic influences. Should the climate change, the accomodation between the host and the parasite may be disturbed.

Amongst the parasites of livestock there are examples of species whose transmissibility is known to be affected by climate. The larvae of *Haemonchus contortus*, a gastro-intestinal parasite of sheep, require mean temperatures > 18°C for normal development, whereas the development of *Ostertagia circumcincta* larvae is suppressed above 15.5°C. As both require moisture, the former is an organism of summer rainfall areas, and the latter of winter rainfall areas (Southcott *et al.* 1976).

There is less known about the parasites of Australian native vertebrates, and most of the published investigations have been taxonomic (e.g. Beveridge & Durette-Desset 1992). Arundel *et al.* (1990) undertook one of the few epidemiological studies, which demonstrated that helminth parasites can cause considerable mortality in Eastern Grey Kangaroos, and concluded that development of free-living larvae is influenced by climate. In North America, the Moose *Alces alces* can exist sympatrically with White-tailed Deer *Odocoileus virginianus* only in those areas where circumstances do not favour persistence of infective larvae of the meningeal worm *Parelaphostrongylus tenuis* (Gilbert 1992). Hence, climate change may indirectly influence the distributions of terrestrial vertebrates through its effect on the probability of disease transmission.

Mechanisms for coping with climate change

Possingham (1993) recognised that there are three means by which a species might survive climate change – range change to track shifting climate zones, tolerance of the change, and/or microevolutionary change. Examples are presented which demonstrate that tolerance in the form of behavioural plasticity may counter climate change, but tracking appears implausible for many small terrestrial species.

Tolerance

The Red Fox (*Vulpes vulpes*) has a complex social structure which can be modified to cope with environmental change. Zabel & Taggart (1989) have demonstrated an effect by the *El Niño* phenomenon on the food supply of a population of foxes on Round Island, Alaska. Increased water temperatures in the Bering Sea were associated with widespread nesting failure in the seabird species which comprise most of the summer diet of the foxes. Resorption and preimplantation loss are known to occur in pregnant vixens (Ryan 1976), a common cause of which is nutritional stress (see Moustgaard 1969). Hence, if the available food was uniformly distributed amongst the foxes, total reproductive failure in the fox population

may well have occurred. However, on Round Island, dietary changes to smaller, less common, and less accessible seabird species were associated with changes in the social structure of the foxes. Polygyny, the reproductive mode prior to the dietary change, was supplanted by monogamy. The male's help is essential for capturing and delivering prey to a lactating female and her litter (Kleiman 1977); thus the change in the social structure meant that assistance provided by the male fox was focussed on fewer cubs at a time when it would have been more difficult for the males to procure food. Individual reproductive success (in terms of cubs reared to sexual maturity) of the reduced number of breeding females was not significantly affected by the *El Niño* phenomenon. Hence, a (temporary) climate change which lead to total reproductive failure of the two seabird species most prominent in the diet of the foxes did not in turn lead to total reproductive failure in the foxes.

The Eastern Long-necked tortoise (*Chelodina longicollis*) has simpler behavioural patterns than the Red Fox, but still has some plasticity. It appears to adjust its selection of nesting sites to take account of meteorological parameters likely to affect incubation temperature. At Armidale, New South Wales, the species digs nesting chambers in unshaded areas, which increases insolation and hence egg temperature, and shortens incubation (Parmenter 1976). The same species at Roseworthy, South Australia, digs about two-thirds of its nests in sites shaded for more than half of the day (Stott 1987, 1988). Nest temperatures were not recorded at either site, but mean daily temperatures during the incubation period are higher at Roseworthy (3.9°C higher in January) and cloud cover is less frequent (0.7 oktas less in January). Thompson (1988b) has demonstrated that unshaded nests of *Emydura macquarii* at Barmera, South Australia can be 2.6°C warmer than shaded nests, and attributed deaths in some unshaded nests to excessive heat. Thus it is reasonable to speculate that *C. longicollis*, like the species of testudines considered by Bull *et al.* (1982) and Schwarzkopf & Brooks (1987), positions its nests relative to shade to obtain optimum subsurface temperatures for incubation.

Tracking

Baker *et al.* (1992) dated late Holocene vegetation changes at two sites in Iowa which correspond to a rate of retreat of prairie of 300-600m per annum. However, the anticipated rate of anthropogenic climate change is much greater than in the past (Possingham 1993). With the low relief of the inland plains of northern South Australia, mean thermal gradients are slight, and a typical distance between isotherms corresponding to the predicted annual rate of temperature change of 0.03°C is 2000 m. Because many bird species of the Australian arid zone are nomadic (Wiens 1991), tracking climate change is physically and behaviourally possible. However, sedentary species may have behavioural difficulties. Few data are available on the dispersal capability of small terrestrial vertebrates, but the longest dispersal movement recorded by James (1991c) for any individual of five species of *Ctenotus* was 605m, indicating that unassisted dispersal is most unlikely to be able to track climate change at the predicted rate.

Possingham (1993) points out that comparisons of dispersal capability with the rate of climate change may be simplistic. The comparison is useful to identify species which are physically incapable of tracking climate, but cannot by itself determine competence. There must be subsequent stages in the process of identifying species at risk, such as consideration of physical barriers and inter-relationships between species. Even if *Ctenotus* spp. were physically capable of tracking climate change, there is a close and presumably obligatory association between many species of *Ctenotus* and *Triodia* and *Plectrachne* spp. (spinifex grasses) and their attendant termites. These are primarily distributed in infertile, sandy soils (Graetz *et al.* 1988), which indicates that spinifex-dependent species of *Ctenotus* which are less tolerant of increased temperatures would be unable to track climate change across changes in soil fertility and type. For vertebrates in the north of South Australia, tracking temperature changes means a generally southern extension in range (with or without a northern contraction, a separate issue which would depend on the upper limits of tolerance), but for *C. pantherinus* there would be constraints because long distance dispersal or even local spread of *Triodia* and *Plectrachne* seem to require considerable time (Jacobs 1982). Also, these grasses would not extend into heavy clay soils and limestone plains, the latter being generally south of the present distribution of *C. pantherinus*.

The steepness of climatic gradients in mountainous areas is much greater than on plains, and thus altitudinal tracking of climate change is much more feasible than latitudinal tracking for small terrestrial vertebrates. Generally, a short climb in altitude corresponds to a major shift in latitude (Peters & Darling 1985). Over a distance of about 15 km in the Adelaide Hills, a 500m increase in altitude is associated with a fall in January mean maximum temperature of about 5°C, and a rise in mean annual rainfall of about 600 mm. However, whilst the climate as one component of a species' environment may track up a mountain, other components of the environment may be fixed; for example, substrate structure and fertility usually change with altitude.

To allow tracking requires the linking of areas managed primarily for conservation along latitudinal and altitudinal gradients (Norton 1990). The review

of nature reserves in south-eastern New South Wales undertaken by Margules & Stein (1989) confirmed that a single, long, narrow, rectangular reserve aligned along an altitudinal gradient would be the configuration which would most parsimoniously meet the dominant environmental requirements of temperature, rainfall, and substrate for 26 canopy tree species which occur in the region. Mackey *et al.* (1988) note the necessity and argue the validity of using vegetation data as surrogates for data on fauna habitat in the present circumstances of paucity of the preferred primary data, and advocate a focus on ecological gradients in order to provide a margin of safety in assessing areas for conservation value. However, because of the low relief of much of South Australia, only latitudinal gradients are possible in most areas.

Conclusion

The paper has focused on a number of studies which have relevance to the issue of climate change. On reviewing the topic, it is apparent that the zoological base from which changes may be predicted is imperfect. Reliable information on the present distribution, abundance, population dynamics, and interspecific relationships of Australian vertebrates is limited (Norton 1990), but there is sufficient information to indicate that climatic influences on the distribution of many animals operate through mechanisms which are subtle and as yet poorly understood, and sufficient information to warrant a conclusion that climate change of any magnitude is quite likely to affect the distributions of many species of terrestrial vertebrates.

Conclusions about the fate of individual species are at present speculative. Deterministic studies such as those undertaken on kangaroo populations are less speculative than mechanistic studies because of the complexity of the means by which climate influences the biota, but mechanistic examinations are complementary in that they may reveal critical aspects of detail not apparent to deterministic considerations.

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